

**A NEW TRIBAL PLACEMENT FOR THE AUSTRALASIAN
GENERA *HOMETHES* AND *AEOLODERMUS*
(COLEOPTERA: CARABIDAE: ODACANTHINI)**

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Abstract.—*Homethes* Newman and *Aeolodermus* Andrewes are removed from tribe Platynini and placed in Odacanthini based on synapomorphies of the male terminalia and female reproductive tract. Cladistic analysis based on 25 internal and external morphological characters of 11 odacanthine taxa supports *Scopodes* Erichson as the sister-group to the clade of *Homethes* + *Aeolodermus*, and corroborates the synonymy of tribe Pentagoncini with Odacanthini.

Key Words.—Insecta, Odacanthini, *Homethes*, *Aeolodermus*, cladistics

In 1842, when Edward Newman described *Homethes elegans* as the single member of a new genus, he commented “This elegant little insect somewhat resembles *Anchomenus pallipes*.” Over the ensuing 149 years, *Homethes* has remained misclassified, being variously considered a member of the tribes Lebiini and Platynini; the latter tribe containing *Anchomenus*. Shared derived characters of the male and female reproductive structures allow a corrected taxonomic placement for *Homethes* and the related *Aeolodermus* Andrewes. In this paper, I review the classificatory history of these two genera, and illustrate the male terminalia and female reproductive tract for *Homethes guttifer* Germar and *Aeolodermus emarginatus* Chaudoir. Cladistic interpretation of male terminalic and female reproductive tract characters necessitates transfer of both genera from the Platynini to the Odacanthini sensu Liebherr (1988). Cladistic analysis using a data set modified from Liebherr (1988) is used to place *Homethes* and *Aeolodermus* within the Odacanthini. *Scopodes* Erichson is suggested as the sister-group to *Homethes* + *Aeolodermus*. Biogeographic consequences for the Platynini are reviewed in light of this taxonomic adjustment.

MATERIALS AND METHODS

Specimens of *Homethes* and *Aeolodermus* were relaxed in near-boiling soapy distilled water, dissected, and cleared overnight in cold 10% potassium hydroxide. After clearing, the pH of dissected parts was neutralized using dilute acetic acid. Male terminalia were placed directly into glycerin for examination. Female reproductive tracts were stained in chlorazol black® in methyl cellulose, and mounted on temporary glycerin microslides. Phase-contrast compound microscopy was used from $\times 40$ to $\times 400$ for examination of female reproductive structures. All dissected parts are stored in plastic glycerin vials under the pinned specimens.

Cladistic analysis was used to establish placement of the two genera within the Odacanthini by adding them to a data set extracted from Liebherr (1988). In that study, nine odacanthine taxa were used as out-groups for an analysis of West Indian Lachnophorini. For this study, the nine odacanthine taxa plus *Homethes*

guttifer and *Aeolodermus emarginatus* were considered the in-group, and characters were polarized assuming Lachnophorini as the sister group to Odacanthini (see Liebherr 1988: fig. 7). Twenty-five characters (Table 1) proved cladistically informative in the new 11-taxon data set (i.e., the derived condition of the characters was represented in more than one but less than all of the taxa of the in-group). Twenty-two of these characters, herein numbered 1, 2, 4–22, and 25, were derived from Liebherr (1988). The primitive and derived states of these characters are given in Liebherr (1988), with the appropriate character numbers from that publication listed in Table 1. Three more characters are new additions to the data set: character 3—temples behind eyes moderately developed (0 = primitive), temples elongate, neck quite constricted (1 = derived); character 23—spermathecal gland spherical (0), gland bipartite (1) (Figs. 1, 4, 7); character 24—lumen of bursa copulatrix glabrous or with fine microtrichia (0), lumen with short, stout spines (1) (Figs. 1, 4, 7). One character coding was changed from Liebherr (1988); *Eudalia latipennis* was coded for the derived state of character 22.

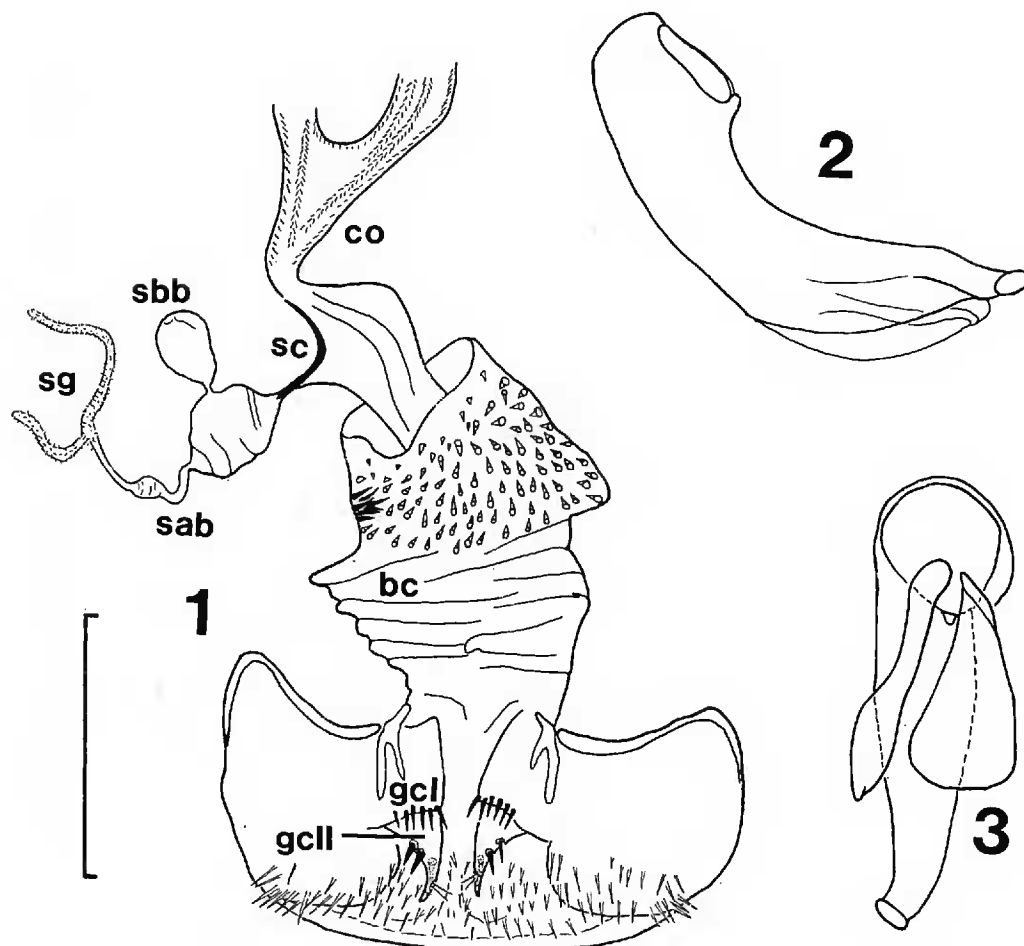
Cladistic analysis was conducted using the Hennig86 computer package (Farris 1988). The ie* option was used, so that all possible cladogram topologies for the 11-taxon data set were exhaustively searched in order to find the most parsimonious solutions.

CLASSIFICATORY HISTORY

Homethes elegans Newman (1842) was described as the first member of the genus. Chaudoir (1872) adopted an incorrect emended spelling, *Homothes*, proposed by Gemminger & Harold (1868), and described "*Homothes*" *emarginatus*, now the type species of *Aeolodermus*. Chaudoir placed "*Homothes*" immediately preceding *Scopodes* in his paper, but stated that "*Homothes*" and *Stenocheila* Laporte were closely related. MacLeay (1873) and Blackburn (1893) placed *Homethes* amongst the lebiine genera.

Sloane (1920) transferred *Homethes* to the Platynini (his Anchomenini), basing his decision on the uniperforate anterior coxal cavity, and his contention that the male tarsal vestiture was most similar to platynines, and unlike that of the Odacanthini. The former character occurs in the identical state in both the Platynini and Odacanthini. For the latter character, both the Platynini and Odacanthini possess two longitudinal rows of male adhesive squamo-setae (Stork 1980) on protarsal segments 1 to 3. The setal apices are broader in *Aeolodermus* and *Homethes* than in other odacanthine genera, but substantial variation in this trait also occurs throughout the Platynini. Male protarsal setation is thus of ambiguous phylogenetic importance in this case. Sloane (1923: 245) distinguished the Odacanthini from the Platynini by "Head narrowed behind eyes (hardly ever not narrowed). Prothorax narrow (hardly ever wider than head)." Both of these characters are unreliable for diagnosis of the Odacanthini when the numerous characters of the male and female reproductive structures are included in the analysis (Liebherr 1988).

Andrewes (1929) described *Aeolodermus* for the single species *Homethes emarginatus* Chaudoir. He distinguished the genus from *Homethes* by the form of the prothorax and the elytral apex, the upper surface sculpture, and the pubescence of the palpi and tarsi. He followed Sloane in considering both genera members of the Platynini.



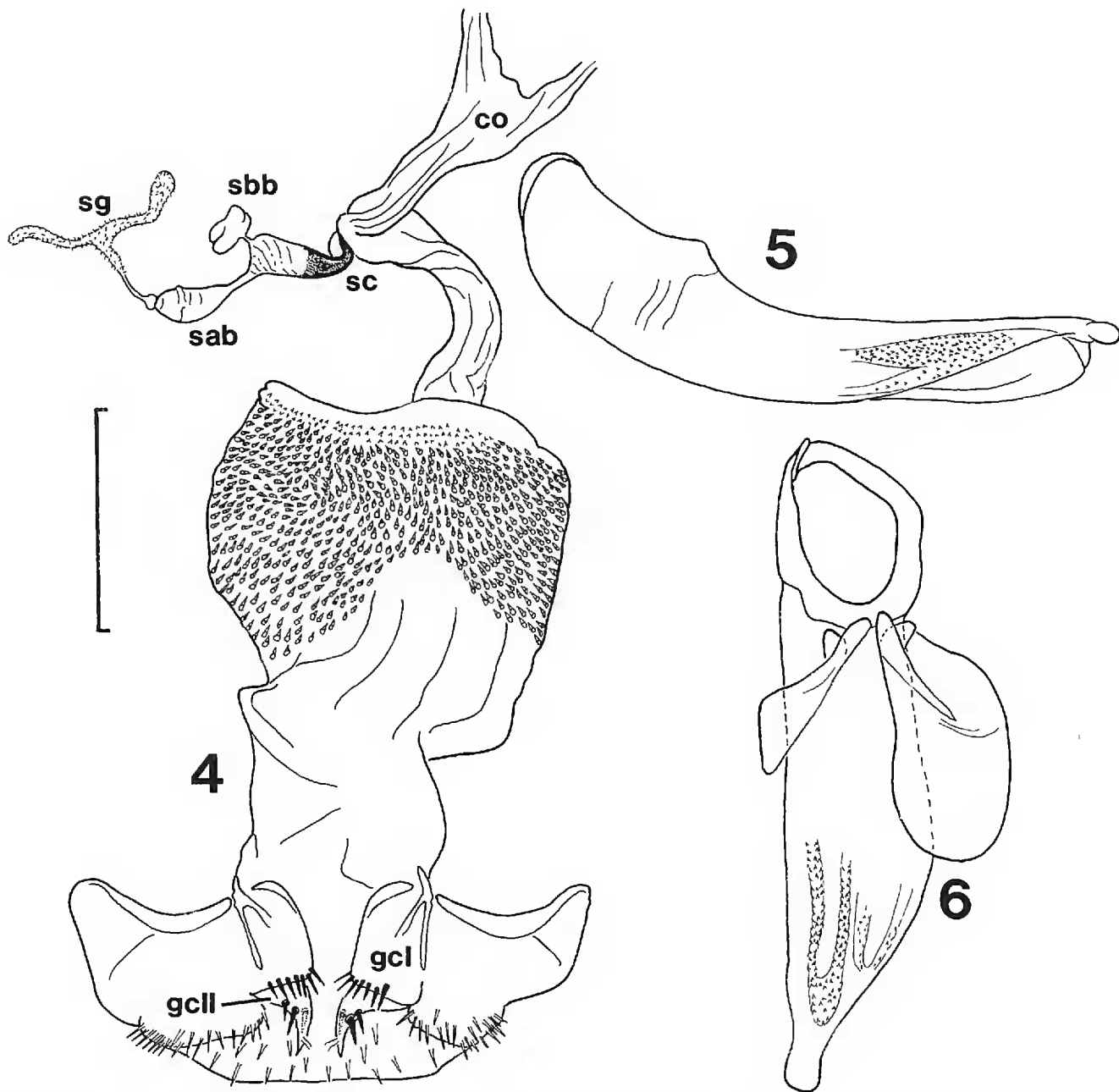
Figures 1–3. *Homethes guttifer* Germar. Figure 1. Female reproductive tract, ventral view. Figure 2. Male aedeagal median lobe, eudextral view. Figure 3. Male aedeagal median lobe and parameres, euventral view. Scale bar = 0.5 mm; bc = bursa copulatrix; co = common oviduct; gcl = basal gonocoxite; gcll = apical gonocoxite; sab = spermathecal apical bulb; sbb = spermathecal basal bulb; sc = U-shaped spermathecal sclerite; sg = spermathecal gland.

Darlington (1956) reviewed the genera of the Platynini (his Agonini) from Australia, listing a total of seven genera native to the continent. Of these, he considered two to be Oriental genera, and one to be a New Guinean genus; all three extending only into northern Australia. A fourth monotypic genus was considered an Australian autochthon, although it too was restricted to northern Queensland. *Colpodes* and *Notagonum*, which he considered genera of convenience, possess Pantropical and New Guinean Indo-Pacific distributions, respectively. Three species of the former and seven species of the latter are known from Australia (Moore et al., 1987). Within Darlington's concept of the Platynini, only *Homethes* exhibits a center of diversity in Australia.

Most recently, *Homethes* was placed in the supertribe Pterostichitae (Moore et al. 1987), with nine species currently recognized from Australia and Tasmania. A tenth species has been described from Java and also recorded from Luzon, the Philippines (Louwerens 1952).

RESULTS AND DISCUSSION

Characters. — The Odacanthini is characterized by a number of synapomorphies of the female reproductive tract that distinguish it from its sister-group, the Lachnophorini, as well as other tribes such as the Platynini, Lebiini, and Ctenodactylini (Liebherr 1988). These include a bipartite spermatheca joined to the common oviduct by a sclerotized, U-shaped duct (Figs. 1, 4, 7), and an elongate, cylindrical bursa copulatrix. All odacanthine genera examined, with the exception of *Odacan-*



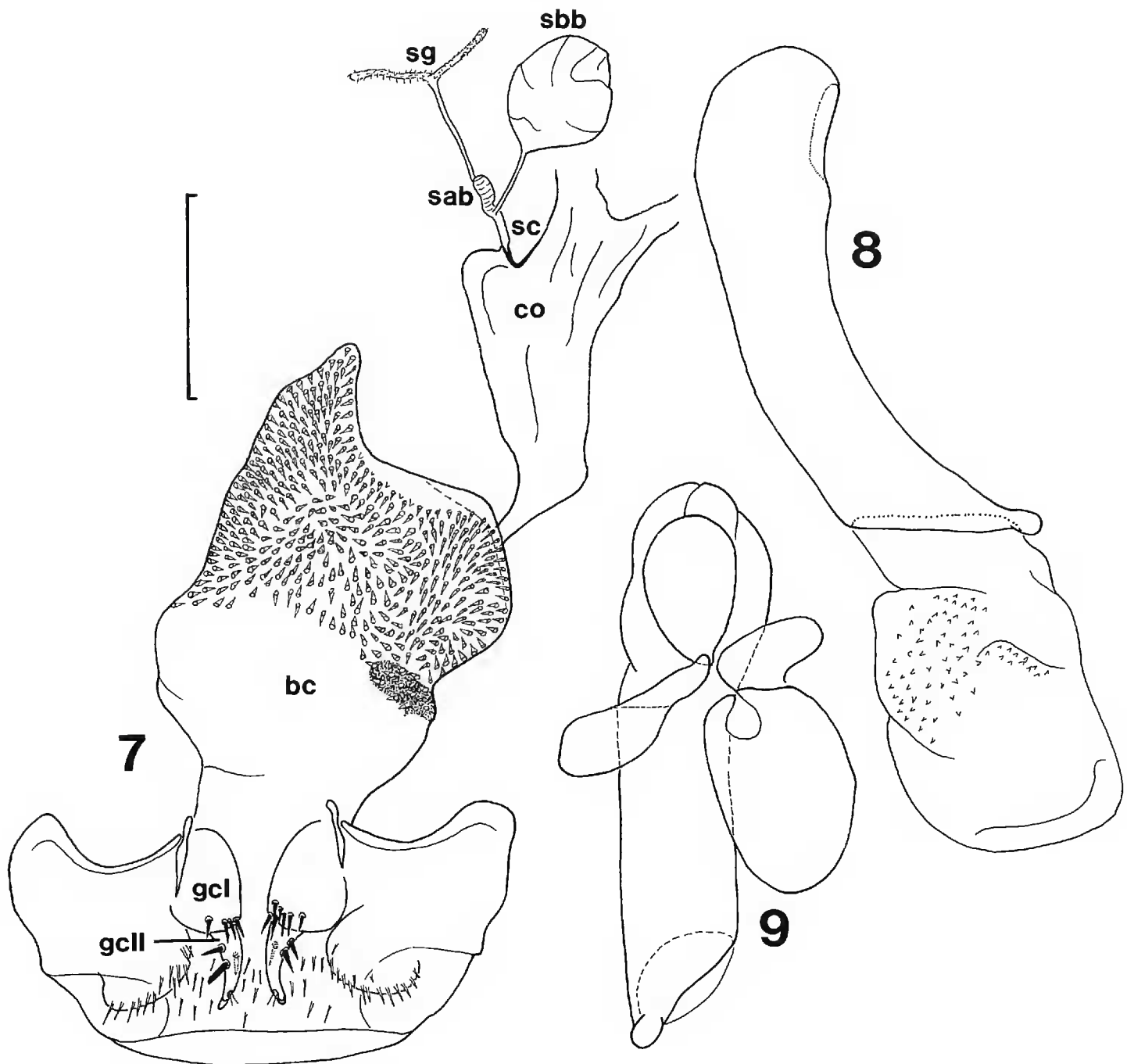
Figures 4–6. *Aeolodermus emarginatus* Chaudoir. Figure 4. Female reproductive tract, ventral view. Figure 5. Male aedeagal median lobe, eudextral view. Figure 6. Male aedeagal median lobe and parameres, euventral view. Scale bar = 0.5 mm; female tract labeled as in Figure 1.

tha, possess the synapomorphy of spermathecal basal bulb narrowed basally, usually connecting with the spermathecal base via a thin duct.

The male aedeagus of the Odacanthini is also cladistically diagnostic, exhibiting the following derived character states: (1) apex of median lobe moderately straight, the lobe not crescent shaped (Figs. 2, 5, 8); (2) apex of median lobe with a knoblike or with a hooklike process; (3) median lobe curved ventrally near apex, the apex therefore asymmetrical (Figs. 3, 6, 9). In general, the ventral paramere is much smaller than the dorsal one, although taxa within tribes such as the Platynini exhibit this trait in less exaggerated form.

The pygidial defensive gland structure of *Homethes* and *Aeoloermus* is also consistent with membership in the Odacanthini, as the gland reservoir is spherical as observed in other members of that tribe, and lacks the dorsal lobe observed in the Platynini (Forsyth 1972).

The female reproductive tracts of *Homethes guttifer* and *Aeolodermus emarginatus* exhibit several striking, and taxonomically very restricted synapomorphies. The spermathecal gland, which is primitively globose or ovoid when present in carabids, is bipartite (Figs. 1, 4). The basal portion of the luminal walls of the



Figures 7–9. *Scopodes aeneus* MacLeay. Figure 7. Female reproductive tract, ventral view. Figure 8. Male aedeagal median lobe, internal sac distended, eudextral view. Figure 9. Male aedeagal median lobe and parameres, euventral view. Scale bar = 0.5 mm; female tract labeled as in Figure 1.

bursa couplatrix are covered with strong spinose teeth. The only other taxon in which I have observed these derived character states is *Scopodes aeneus* MacLeay (Fig. 7).

Homethes and *Aeolodermus* do not possess the dorsal habitus of many taxa traditionally placed in the Odacanthini, as their pronota are not narrow and cylindrical, and their necks are not strongly constricted. However, the former character is also not diagnostic for taxa long included in the Odacanthini (e.g., *Eudalia* Laporte). Pronotal shape is usefully diagnostic at the species level, but may change quite drastically even among closely related species (Liebherr 1986), and should be discounted when judging cladistic affinity. A constricted neck is exhibited by most odacanthines, with *Scopodes* a notable exception. That *Scopodes* shares several other synapomorphies with *Homethes* and *Aeolodermus* suggests that their broad necks may be the result of relatively recent common ancestry.

Cladistic Analysis.—The 11 taxa and 25 characters (Table 1) may be arranged on three equally parsimonious cladograms of 46 steps, each possessing a consis-

Table 1. Taxon \times character data matrix for cladistic analysis of 11 odacanthine taxa using 25 characters; 0 = primitive state, 1 = derived. Out-group assumed represented by all 0-state characters.

Character No. used here Character No. in Liebherr (1988)	Characters																								
	1 7	2 9	3 —	4 10	5 11	6 12	7 13	8 15	9 16	10 17	11 18	12 19	13 20	14 21	15 22	16 23	17 24	18 26	19 29	20 30	21 34	22 44	23 —	24 —	25 50
<i>Eudalia latipennis</i> MacLeay	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	1
<i>Pentagonica picticornis</i> Bates	0	1	0	1	0	0	1	0	1	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1
<i>Scopodes aeneus</i> MacLeay	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1	1	1	0
<i>Lachnothorax</i> sp.	1	1	0	0	1	1	0	1	0	0	0	1	0	0	0	1	0	0	0	0	1	1	0	0	0
<i>Dicraspeda brunnea</i> Chaudoir	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0
<i>Odacantha melanura</i> L.	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>Colliuris pensylvanicus</i> L.	0	1	1	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	1	1	1	0	0	0
<i>Colliuris</i> sp.	1	1	1	0	1	1	0	1	0	1	1	1	1	0	1	0	0	1	1	0	1	1	0	0	0
<i>Colliuris hubenthali</i> Liebke	0	1	1	0	0	0	0	1	0	1	0	1	1	0	1	0	0	1	1	0	0	1	0	0	0
<i>Homethes guttifer</i> Germar	0	0	0	1	0	0	0	1	1	1	0	0	0	0	0	1	1	0	1	0	0	1	1	1	0
<i>Aeolodermus emarginatus</i> Andrewes	0	0	0	1	0	0	0	1	1	1	0	0	0	0	0	1	1	0	0	0	0	1	1	1	0

tency index of 0.54, and a retention index of 0.60 (Farris 1989). Taking the strict consensus of the three cladograms (Fig. 10), which is also one of the three initial cladograms produced, *Odacantha* is the cladistically most basal taxon of the 11. The other 10 taxa are divided into two clades; the one of interest here composed of *Pentagonica*, *Scopodes*, *Homethes*, and *Aeolodermus*. *Homethes* and *Aeolodermus* are integral members of the Odacanthini based on this analysis. They share four synapomorphies with *Scopodes*: character 2—a broad neck (considered a reversal from the constricted state); character 17—dorsal elytral setal impressions foveate; character 23—spermathecal gland bipartite; and character 24—bursal luminal wall of bursa copulatrix with stout spinose teeth. *Homethes* and *Aeolodermus* can be distinguished cladistically from *Scopodes* by three character-state advances and from none to two reversals depending on character optimization. The advances include: character 8—integument with fine pelage of microsetae; character 9—pronotal base with recurved margin and median lobe; and character 16—more than three setae in the third elytral interval. The reversals to the primitive state potentially include: character 7—mentum with distinct mentum suture; 14—pronotal margin not angled at the position of the lateral seta. Alternatively, the derived states for these characters—mentum not separated from gula by a suture, and pronotal lateral margin angulate—may have arisen independently in *Pentagonica* and *Scopodes*. At least for character 14, the former scenario may be preferred, because some specimens of *Aeolodermus emarginatus* exhibit a slight angulation at the lateral seta. Other specimens do not, however, and in any case the angulation is not pronounced. As mentioned above, pronotal shape is often phylogenetically plastic, and reversals or parallelisms should not be unexpected in evolution of this structure.

In this analysis, *Scopodes aeneus* is cladistically distinguished from *Homethes* and *Aeolodermus* by the presence of a laterobasal pronotal seta (a reversal of character 10), and by punctate elytral striae (character 21). *Scopodes* spp. from New Guinea vary in both characters; the laterobasal pronotal seta may be present or absent, and elytral striae are either present and impunctate, or much reduced (Darlington 1968). *Scopodes* is separable from the other two genera by its extremely convex compound eyes, considered an autapomorphy in this analysis.

The only character state difference between *Aeolodermus* and *Homethes* in this data set is the possession of the derived state for character 19 by *Homethes guttifer* (elytra with testaceous maculae on a darker ground color). This character is not diagnostic for all *Homethes* species, as a number of them have uniformly colored elytra. The characters cited by Andrewes (1929) as diagnostic for *Aeolodermus* (see Classificatory History section) may be autapomorphies of this species, and it is possible that *Homethes* is a paraphyletic taxon containing *Aeolodermus*. Moreover, as *Scopodes* can be reliably separated from *Aeolodermus* and *Homethes* only by eye development, the latter two genera should be cladistically analyzed in concert with a number of *Scopodes* species, as well as the closely related monotypic genera *Parascopodes* Darlington and *Actenonyx* White (Darlington 1968), in order to reliably determine the relationships of all genera in this complex.

Taxonomic and Biogeographic Consequences.—Based on the cladistic analysis, *Homethes* and *Aeolodermus* are not properly placed in the Platynini. All characters of the male and female reproductive and copulatory structures examined point to membership in the Odacanthini. Removal of these genera from the Platynini

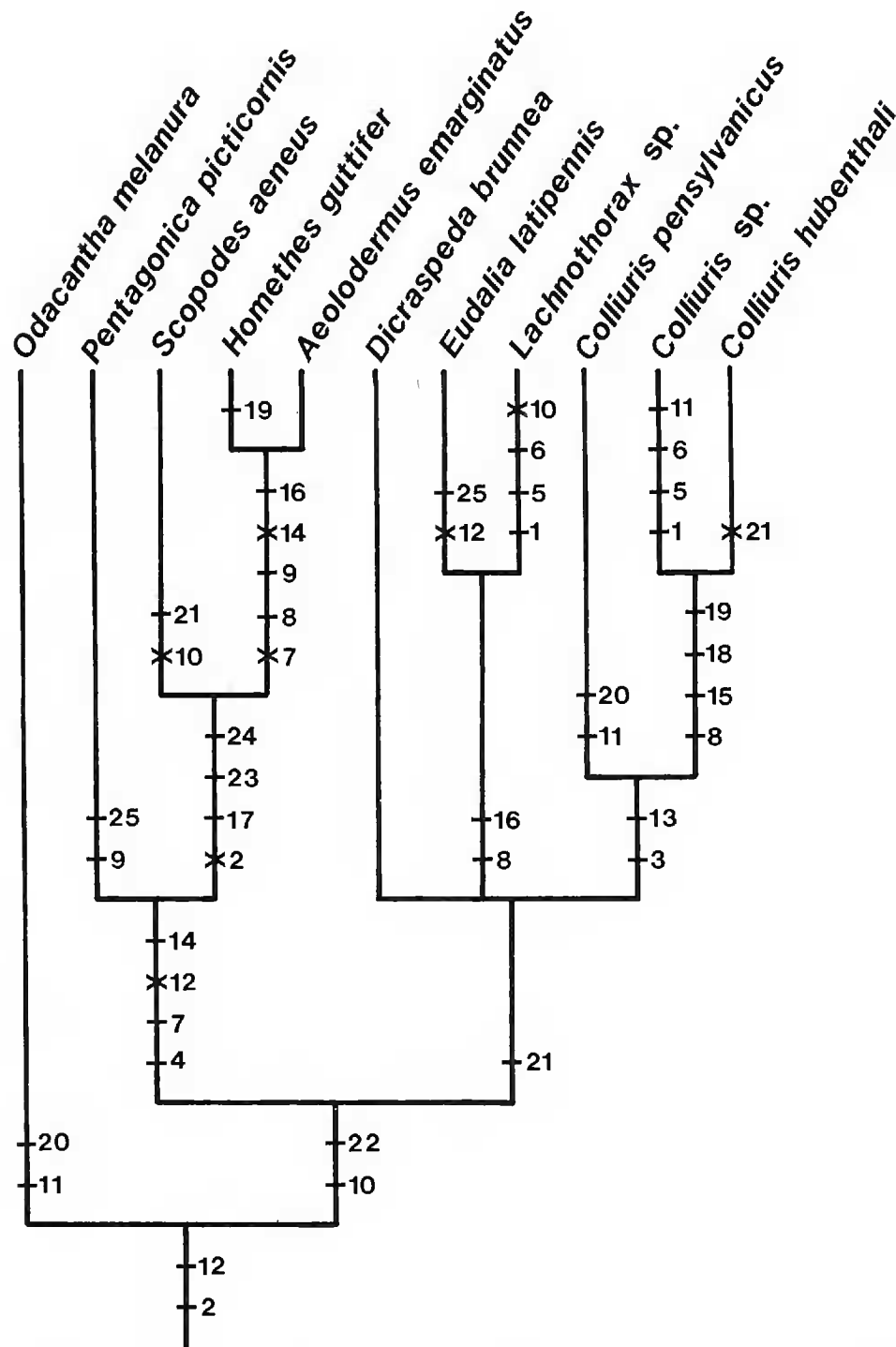


Figure 10. Consensus cladogram (and 1 of 3 equally parsimonious cladograms) for the 11 exemplar taxa of Odacanthini. Character-state advances shown by slashes, reversals shown by "x"'s. Other two equally parsimonious cladograms resolve trichotomy so that either *Dicraspeda*, or *Eudalia* + *Lachnothorax* are sister groups to *Colliuris*.

reduces the presence of that tribe in the Australian biota. The remaining genera of the Platynini in Australia can be characterized either by being restricted to New Guinea or southeast Asia plus northern Australia, or by being widely distributed and quite diverse, with only a few member species in Australia (Darlington 1956). No generic-level platynine taxon possesses a distribution centered on Australia. Without knowing the cladistic relationships within taxa including Australian species, definitive biogeographic conclusions are not possible. However, it appears likely that platynine taxa present in Australia are derived from Oriental or Indo-Malayan groups with Tertiary relationships to New Guinea and the Indonesian islands, or from members of more recent groups with Pleistocene connections to New Guinea (MacKerras 1970).

The close relationship between *Homethes*, *Aeolodermus*, and *Scopodes* is strong-

ly supported by the highly unusual synapomorphies observed in the female tracts. *Scopodes* is distributed on Java, New Guinea, New Caledonia, New Zealand, and Australia (Moore et al. 1987). The strongly overlapping geographic distributions of the three genera suggest either extensive dispersal during the divergence of these taxa, or paraphyly of one or more of the genera relative to another.

The establishment of the clade of *Scopodes* + (*Homethes* + *Aeolodermus*) corroborates the synonymy of the tribe Pentagonicini with Odacanthini. Of genera in the above analysis, *Scopodes* and *Pentagonica* have been traditionally included in Pentagonicini (e.g., Moore et al. 1987), based on the angulate lateral margin of the pronotum. *Homethes* species exhibit convexly rounded pronotal margins, and *Aeolodermus emarginatus* has variably rounded to slightly angulate margins. The clade containing these taxa (Fig. 10) thus has angulate, variably angulate, and rounded pronotal margins represented in the member taxa. In Liebherr (1988), the tribe Pentagonicini was synonymized with the Odacanthini, because recognition of the Pentagonicini would have rendered the Odacanthini paraphyletic. By the current cladistic scheme, the taxa previously placed in the Pentagonicini also comprise a paraphyletic group. Therefore, recognition of the Pentagonicini based on this analysis would involve recognition of two paraphyletic groups, clearly an undesirable and unnecessary alternative.

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